Biometrics 59, 778–785
December 2003

Demographic Analysis from Summaries of an Age-Structured Population

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Summary. Demographic analyses of age-structured populations typically rely on life history data for individuals, or when individual animals are not identified, on information about the numbers of individuals in each age class through time. While it is usually difficult to determine the age class of a randomly encountered individual, it is often the case that the individual can be readily and reliably assigned to one of a set of age classes. For example, it is often possible to distinguish first-year from older birds. In such cases, the population age structure can be regarded as a latent variable governed by a process prior, and the data as summaries of this latent structure. In this article, we consider the problem of uncovering the latent structure and estimating process parameters from summaries of age class information. We present a demographic analysis for the critically endangered migratory population of whooping cranes (*Grus americana*), based only on counts of first-year birds and of older birds. We estimate age and year-specific survival rates. We address the controversial issue of whether management action on the breeding grounds has influenced recruitment, relating recruitment rates to the number of seventh-year and older birds, and examining the pattern of variation through time in this rate.

Key words: Age-structured populations; Demographic analysis; Latent variables; Markov chain Monte Carlo; Whooping cranes; Wildlife statistics.

1. Introduction

Age-structured population models form the basis of many studies of animal populations, and are employed as a tool to facilitate the conservation and management of a number of animal species of special interest, such as whales (Breiwick, Eberhardt, and Braham, 1984), waterfowl (Johnson et al., 1997), and sea turtles (Crouse et al., 1987). These models are used to assess population growth rate, minimum viable population size, and the effects of harvest or other human-induced impacts, and to study theoretical questions of relevance to population and evolutionary biology (Caswell, 2000). Data used in the analysis of age-structured population models usually consist of individual life histories, or counts of individuals within age classes. However, it is not always feasible to collect such data. On the other hand, it is often relatively simple to identify individuals as belonging to groups that are aggregations of one or more age classes (typically juvenile/adult). For example, many birds and mammals can be identified as juveniles based on plumage, coloration, and other physical characteristics which may be assessed in the field. These aggregate classes are sometimes used as the basis of age-structured population models and may be sufficient for many purposes. Generally, however, a more detailed model of population age structure and vital rates is desirable and biologically realistic. To the best of our knowledge, methods for estimating general age-structured population models from aggregate age class data have not been developed.

In this article, we present a framework for estimating age-structured population models from aggregate age class data, motivated by data collected on endangered whooping cranes (*Grus americana*). The key idea behind our approach is to employ an age-structured population model to describe the underlying process that gave rise to the aggregate age-class data. Raftery, Givens, and Zeh (1995) employ a similar idea in the analysis of a deterministic population model for bowhead whales. A similar development can also be found in recent geophysical applications (e.g., Wikle et al., 2001), where observations of a state variable are available, and where an underlying process model is constructed from physical considerations.

2. Whooping Cranes

The whooping crane is one of the rarest and most endangered birds in North America. Currently, there is only one natural migratory population. This population migrates between wintering grounds in Aransas National Wildlife Refuge, Texas, and breeding grounds in Wood Buffalo National Park, Canada (Kuyt, 1995, 1996). There are also several captive populations, established by collecting fertile eggs from the wild population and rearing them in captivity. In addition, a nonmigratory population has been established by releasing captive-bred individuals in Florida (Nesbitt et al., 2001), and attempts at establishing an eastern migratory population are underway (Horwich, 2001).

Although the Aransas/Wood Buffalo migratory population was down to as few as 16 individuals in 1941, the most recent census of this population counted a total of 176 individuals, of which 15 were juveniles (i.e., less than one year old) and 161 were adults or subadults (Tom Stehn, personal communication). This census has occurred annually since 1938. It provides a total count of the individuals in the population each year when the birds arrive on their wintering grounds in Texas (Binkley and Miller, 1980, 1983; Boyce and Miller, 1985). Juveniles (those with brown in their plumage) are tallied separately from adults and subadults (those with white plumage), but since the age of white birds cannot be assessed, there is no direct information about population age structure through time. Our primary goal in this article is to estimate the parameters of an age-structured population model from these age-class summaries.

Management decisions concerning this population are critical to the survival of the species. One such decision concerns whether to manipulate eggs in the nests of the migratory population. Prior to 1967, no egg collection was performed, but after that year, fertile eggs have been collected from some nests for the establishment of the captive populations (Kuyt, 1995, 1996). Occasionally, a single egg has been taken from nests with 2 fertile eggs, and substituted for an infertile egg in a nest with no fertile eggs. Because whooping cranes only rarely raise 2 young to fledging, it was assumed that egg manipulation would have little or no effect on the migratory population (Lewis, 2001). Currently, there is some debate about the effect of the manipulation of eggs on the migratory population (Cannon, Johns, and Stehn, 2001; Ellis and Gee, 2001; Lewis, 2001) and concern that this action might be harmful to the wild population. Cannon et al. (2001) performed a two-sample t-test on the annual percent recruitment, concluding that mean recruitment was significantly lower in years in which egg collection occurred. Ellis and Gee (2001) argued that egg collection was not harmful, and may actually be beneficial to the population. These attempts to address the effect of egg collection have not taken into account the age structure of the population.

Binkley and Miller (1980) modeled age-specific survival with regression of numbers of white birds (W_i) on previous counts of brown birds (B_i), using the relation

$$E\left(W_i\right) = \sum_{x=1}^{T} S(x) B_{i-x},$$

where $S(x)$ is the probability that an individual lives at least x years. After specifying a maximum lifetime T and a parametric form for the survival function, they discard the first T counts of white birds, and fit the model by least squares. To attain a linear model, they worked with polynomial functions of survival, choosing a quadratic as their best approximation. Questions of the appropriateness of a polynomial survival model aside, the absence of an explicit description of the covariance structure among and between response variables and regressors, and the necessity of discarding data limit the appeal of their analysis.

Our primary goal in this paper is to perform a demographic analysis of the Aransas/Wood Buffalo whooping crane data, with explicit modeling of the latent age structure of the population. A secondary goal is to evaluate the evidence these data provide regarding the effects of egg collection on recruitment, i.e., on the number of brown birds in the following year.

3. Model

The models we consider include demographic parameters for 7 distinct age classes. The first 6 age classes correspond to the first 6 years of life, the seventh consists of birds in their seventh year or older. Most of the age class 7 birds are breeders (roughly 90%), as are a few of the age class 6 birds (roughly 30%); breeding is uncommon and rarely successful among younger birds (George Gee, personal communication). The median lifespan for whooping cranes has been variously estimated at 6–7 years (Kuyt and Goosen, 1987) and 8–9 years (Binkley and Miller, 1980); Binkley and Miller assumed a maximum age of 23 years, though we note that a bird in captivity at the Patuxent Wildlife Research Center recently died at age 38.

The number of age class j birds in year i is Y_{ij}. We denote the age distribution in year i by $\boldsymbol{Y_i} = (Y_{i1}, Y_{i2}, \ldots, Y_{i6}, Y_{i7})'$, and refer to the $n \times 7$ matrix $\boldsymbol{Y} = (\boldsymbol{Y_1}, \boldsymbol{Y_2}, \ldots, \boldsymbol{Y_n})'$ as the population history. Most of the numbers Y_{ij} are unknown; our analysis is based on data

$$B_i = Y_{i1} = \text{number of brown birds in year } i,$$

and

$$W_i = \sum_{j=2}^{7} Y_{ij} = \text{number of white birds in year } i,$$

$i = 1, 2, \ldots, n = 64$ (1938–2001), summarized by $\boldsymbol{B} = (B_1, B_2, \ldots, B_n)'$ and $\boldsymbol{W} = (W_1, W_2, \ldots, W_n)'$. Data for 1938 to 1999 come from Cannon et al. (2001), the remaining years of data and a correction to the 1996 data were provided by the U.S. Fish and Wildlife Service (Tom Stehn, personal communication). These data are presented in Table 1.

Changes in the age distribution through time are naturally modeled by a first order Markov chain, as indicated in Figure 1. Age class 1 individuals in year i have annual survival probability φ_{i1}; those that survive make up age class 2, in year $i+1$. We model this transition by specifying that given Y_{i1}, $Y_{(i+1)2}$ is a binomial random variable, with index Y_{i1} and success parameter φ_{i1}. Similarly, we model $Y_{(i+1)(j+1)}$ as binomial, with index Y_{ij} and success parameter φ_{ij}, for $j = 2$, 3, 4, 5. Age class 7 consists of survivors from the previous year's age classes 6 and 7, hence $Y_{(i+1)7}$ is modeled as a binomial random variable, with index $Y_{i6} + Y_{i7}$ and success parameter φ_{i6}.

We model the recruitment by assuming that $Y_{(i+1)1}$ is a Poisson random variable with mean $\lambda_i Y_{i7}$. We refer to the parameter λ_i as the per-breeder recruitment rate for year i, noting that the designation is only approximately correct: Y_{i7} is an index to the number of breeders in year i, rather than the exact number. Heterogeneity due to this indexing is a component of the temporal variation of λ_i.

Table 1
Numbers of brown (B) and white (W) birds in the wintering population of whooping cranes at Aransas. Egg-collection years are in bold.

Year	B	W	Year	B	W	Year	B	W	Year	B	W
1938	4	14	1954	0	21	1970	6	51	**1986**	21	89
1939	7	15	1955	8	20	**1971**	5	54	**1987**	25	109
1940	5	21	1956	2	22	1972	5	46	**1988**	19	119
1941	2	14	1957	4	22	1973	2	47	**1989**	20	126
1942	4	15	1958	9	23	**1974**	2	47	**1990**	13	133
1943	5	16	1959	2	31	**1975**	8	49	**1991**	8	124
1944	3	15	1960	6	30	**1976**	12	57	**1992**	15	121
1945	4	18	1961	5	34	**1977**	10	62	**1993**	16	127
1946	3	22	1962	0	32	**1978**	7	68	**1994**	8	125
1947	6	25	1963	7	26	**1979**	6	70	**1995**	28	130
1948	3	27	1964	10	32	**1980**	6	72	**1996**	16	144
1949	4	30	1965	8	36	**1981**	2	71	1997	30	152
1950	5	26	1966	5	38	**1982**	6	67	1998	18	165
1951	5	20	**1967**	9	39	**1983**	7	68	1999	17	171
1952	2	19	**1968**	6	44	**1984**	15	71	2000	9	171
1953	3	21	**1969**	8	48	**1985**	16	81	2001	15	161

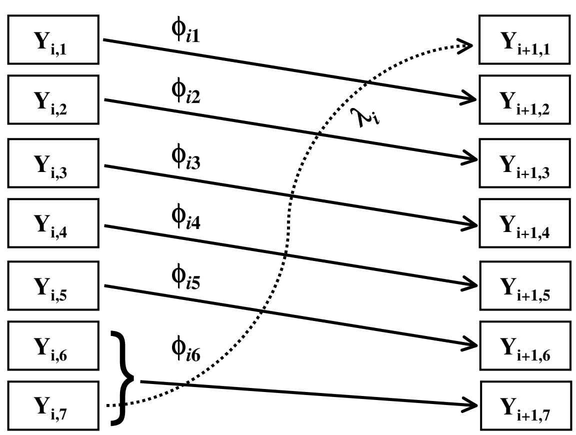

Figure 1. Graphical depiction of whooping crane population model. Rectangles represent age classes $j = 1, 2, \ldots, 7$ for years i and $i + 1$, with arrows indicating stochastic relations in numbers of individuals. The number of age class 1 individuals in year $i + 1$ is a Poisson random variable with mean $\lambda_i Y_{i7}$. For $j = 1, 2, \ldots, 5$, the numbers of age class $j + 1$ individuals in year $i + 1$ are binomial random variables, with rate φ_j and index Y_{ij}. Individuals in age classes 6 and 7 have a common survival rate φ_6.

4. Analysis

Since the data $(\boldsymbol{B}, \boldsymbol{W})$ are a time series, it is natural to conduct analysis having conditioned on the first year's data. Let $[C \mid D]$ denote the conditional probability of C given D. It would be reasonable to base inference on a likelihood proportional to $[\boldsymbol{B}, \boldsymbol{W} \mid B_1, W_1]$, which could be obtained by integrating $\boldsymbol{Y}$ out of the joint distribution $[\boldsymbol{Y}, \boldsymbol{B}, \boldsymbol{W} \mid B_1, W_1]$. The first step, then, is to describe $[\boldsymbol{Y}, \boldsymbol{B}, \boldsymbol{W} \mid B_1, W_1]$.

We begin by noting that the conditional distribution of the latent structure $\boldsymbol{Y}$ given the numbers of brown and white birds in year 1 can be written as

$$[\boldsymbol{Y} \mid B_1, W_1] = [\boldsymbol{Y_2}, \boldsymbol{Y_3}, \ldots, \boldsymbol{Y_n} \mid \boldsymbol{Y_1}][\boldsymbol{Y_1} \mid B_1, W_1].$$

Since the data are a function of $\boldsymbol{Y}$, $g(\boldsymbol{Y}) = (\boldsymbol{B}, \boldsymbol{W})$, the joint distribution of latent and observed quantities is

$$[\boldsymbol{Y}, \boldsymbol{B}, \boldsymbol{W} \mid B_1, W_1] = [\boldsymbol{Y_2}, \boldsymbol{Y_3}, \ldots, \boldsymbol{Y_n} \mid \boldsymbol{Y_1}][\boldsymbol{Y_1} \mid B_1, W_1] I(g(\boldsymbol{Y}) = (\boldsymbol{B}, \boldsymbol{W})); \quad (1)$$

the final term on the right hand side of (1) is simply a range-restriction, expressed using an indicator function. Specifically, we may write

$$I\left(g(\boldsymbol{Y}) = (\boldsymbol{B}, \boldsymbol{W})\right) = \prod_{i=1}^{n} I\left(W_i = \sum_{j=2}^{7} Y_{ij}\right) I\left(B_i = Y_{i1}\right). \quad (2)$$

Since $\{\boldsymbol{Y}_i\}$ is modeled as a first-order Markov chain, the first term on the right hand side of (1) can be written as

$$[\boldsymbol{Y_2}, \boldsymbol{Y_3}, \ldots, \boldsymbol{Y_n} \mid \boldsymbol{Y_1}] = \prod_{i=1}^{n-1} [\boldsymbol{Y_{i+1}} \mid \boldsymbol{Y_i}]; \quad (3)$$

further, since we assume that transitions among age classes between years i and $i + 1$ are independent then, given $\boldsymbol{Y_i}$, (3) can be expressed as

$$\begin{aligned}[\boldsymbol{Y_2}, \boldsymbol{Y_3}, \ldots, \boldsymbol{Y_n} \mid \boldsymbol{Y_1}] &= \prod_{i=1}^{n-1} \prod_{j=1}^{7} \left[Y_{(i+1)j} \mid \boldsymbol{Y_i}\right] \\ &= \prod_{i=1}^{n-1} \mathrm{Pois}\left(Y_{(i+1)1}; \lambda_i Y_{i7}\right) \left\{ \prod_{j=1}^{5} \mathrm{Bin}\left(Y_{(i+1)(j+1)}; Y_{ij}, \varphi_{ij}\right) \right\} \\ &\quad \times \mathrm{Bin}\left(Y_{(i+1)7}; Y_{i6} + Y_{i7}, \varphi_{i6}\right), \end{aligned} \quad (4)$$

where $\mathrm{Pois}(x; \mu) = \exp(-\mu)\mu^x / x!$ and

$$\mathrm{Bin}(x; n, p) = \binom{n}{x} p^x (1-p)^{n-x}.$$

The analytical task of integrating $\boldsymbol{Y_2}, \boldsymbol{Y_3}, \ldots, \boldsymbol{Y_n}$ out of (1), so as to obtain a likelihood for parameters $\boldsymbol{Y_1}$, φ_{ij}'s and λ_i's based on the data $(\boldsymbol{B},\boldsymbol{W})$, is prohibitively difficult. Indeed, there may be interest in predicting the unobserved age distribution $\boldsymbol{Y_i}$, and elaborations of the model might require that the latent structure be retained. Our approach, therefore, will be to carry out Bayesian analysis with the latent structure retained, and with diffuse prior distributions on parameters.

The model as described is overparameterized. We thus impose the constraint

$$\text{logit}(\varphi_{ij}) = \alpha_i + \beta_j, \tag{5}$$

where year effects α_i are sampled from a mean-zero normal distribution with precision τ_φ, and age effects β_j are sampled from mean-zero normal distributions with precision parameter $\tau_\beta = 0.40$. Discussion of this choice is deferred, except to note that the prior is sufficiently diffuse to have little effect on inference regarding the β_j's. We model the recruitment parameters as

$$\ln(\lambda_i) = a_{e(i)} + b(i - 32) + \varepsilon_i, \tag{6}$$

where ε_i are independent mean-zero normal random variables with precision τ_λ; subscript $e(i)$ is an indicator of whether year i was an egg-collection year.

Letting $\boldsymbol{\theta} = (\varphi_{ij}, \lambda_i; i = 1, 2, \ldots, 63, j = 1, 2, \ldots, 6)'$ and $\boldsymbol{\psi} = (a_0, a_1, b, \tau_\varphi, \tau_\lambda)'$, we have specified $[\boldsymbol{\theta} \mid \boldsymbol{\psi}]$; the standard noninformative prior $[\boldsymbol{\psi}] \propto (1/\tau_\lambda)(1/\tau_\varphi)$ completes the prior specification for the demographic parameters. We assign a uniform prior to the unknown components of $\boldsymbol{Y_1}$, setting $[\boldsymbol{Y_1} \mid B_1, W_1] \propto c$ to complete the model specification. We thus base our inference on the posterior distribution

$$[\boldsymbol{Y}, \boldsymbol{\theta} \mid \boldsymbol{B}, \boldsymbol{W}] \propto [\boldsymbol{Y}, \boldsymbol{B}, \boldsymbol{W} \mid B_1, W_1, \boldsymbol{\theta}, \boldsymbol{\psi}][\boldsymbol{\theta} \mid \boldsymbol{\psi}][\boldsymbol{\psi}]. \tag{7}$$

We approximate features of the posterior distribution through Gibbs sampling, that is, by cyclical sampling from the full conditional distributions $[\boldsymbol{Y} \mid \cdot] = [\boldsymbol{Y} \mid \boldsymbol{B}, \boldsymbol{W}, \boldsymbol{\theta}, \boldsymbol{\psi}]$, $[\boldsymbol{\theta} \mid \cdot] = [\boldsymbol{\theta} \mid \boldsymbol{Y}, \boldsymbol{B}, \boldsymbol{W}, \boldsymbol{\psi}]$ and $[\boldsymbol{\psi} \mid \cdot] = [\boldsymbol{\psi} \mid \boldsymbol{Y}, \boldsymbol{B}, \boldsymbol{W}, \boldsymbol{\theta}]$; here and throughout, we use notation $[A \mid \cdot]$ to denote the full conditional distribution of A.

5. Gibbs Sampling

5.1 *Gibbs Sampling of Demographic Parameters*

We used the Metropolis-Hastings algorithm for sampling the full conditionals of $\alpha_i, \beta_j, a_0, a_1$, and b; candidate values were generated by adding normally distributed noise to current values. The standard deviations of the candidate generating distributions were selected to yield acceptance rates of 30–40%. We directly sampled the full conditional distributions of τ_φ and τ_λ, which are in the gamma family.

5.2 *Gibbs Sampling of the Population History*

Sampling $[\boldsymbol{Y} \mid \cdot]$ is the most challenging aspect of the analysis. For $i = 2, 3, \ldots, n-1$, the full conditional distribution of $\boldsymbol{Y_i}$ involves two terms from (4) and a term from (2). Thus, $[\boldsymbol{Y_i} \mid \cdot]$ is proportional to

$$\begin{aligned}
&\text{Pois}\left(Y_{(i+1)1}; \lambda_i Y_{i7}\right) \left\{ \prod_{j=1}^{5} \text{Bin}\left(Y_{(i+1)(j+1)}; Y_{ij}, \varphi_{ij}\right) \right\} \\
&\quad \times \text{Bin}\left(Y_{(i+1)7}; Y_{i6} + Y_{i7}, \varphi_{i6}\right) \\
&\quad \times \text{Pois}\left(Y_{i1}; \lambda_i Y_{(i-1)7}\right) \left\{ \prod_{j=1}^{5} \text{Bin}\left(Y_{i(j+1)}; Y_{(i-1)j}, \varphi_{(i-1)j}\right) \right\} \\
&\quad \times \text{Bin}\left(Y_{i7}; Y_{(i-1)6} + Y_{(i-1)7}, \varphi_{(i-1)6}\right) \\
&\quad \times I\left(\sum_{j=2}^{7} Y_{ij} = W_i\right) I\left(Y_{i1} = B_i\right).
\end{aligned} \tag{8}$$

We used the Metropolis-Hastings algorithm to sample the full conditionals of rows $\boldsymbol{Y_i}$ of the $n \times 7$ matrix $\boldsymbol{Y}$. Our candidate-generating distribution was functionally independent of the current value of $\boldsymbol{Y_i}$, subject to the constraints imposed by the data, so that the probability of accepting a candidate value $\boldsymbol{y_i^*}$ to replace the current value $\boldsymbol{y_i}$ was simply

$$p\left(Y_i^*; Y_i\right) = \min\left(\frac{[\boldsymbol{Y_i} = \boldsymbol{y_i^*} \mid \cdot]}{[\boldsymbol{Y_i} = \boldsymbol{y_i} \mid \cdot]}, 1\right). \tag{9}$$

The form of the full conditional (8) imposes certain constraints on acceptable candidate values $\boldsymbol{y_i^*}$. In addition to the explicit constraints imposed by the indicator functions, there are implicit constraints imposed by the ranges of the binomial distributions. Age classes $j = 2, 3, \ldots, 6$ cannot have more individuals than were in age class $j - 1$ in year $i - 1$, nor can age classes $j = 2$, 3, 4, and 5 have fewer individuals than are to be in age class $j + 1$ in year $i + 1$. Any such candidate values would be immediately rejected as having full conditional probability of zero. In the interest of efficient sampling, it is important that candidates be chosen subject to these constraints. The process is illustrated by an example in the Appendix.

6. Alternative Models

We considered a number of restricted versions of the model, which we designated by 4-letter sequences, such as *CABA*. The first letter designates restrictions on the mean structure for the recruitment parameters:

A) $a_0 \neq a_1$, $b = 0$, (egg collection effect, but no temporal trend),
B) $a_0 = a_1$, $b = 0$, (no egg collection effect and no temporal trend),
C) $a_0 = a_1$, $b \neq 0$, (no egg collection effect, but temporal trend),
D) $a_0 \neq a_1$, $b \neq 0$, (egg collection effect and temporal trend).

The second letter describes the existence of annual variation in recruitment parameters:

A) $\varepsilon_i \neq 0$, (there are year effects on recruitment),
B) $\varepsilon_i \equiv 0$, (there are no year effects on recruitment).

The third letter describes the existence of annual variation in survival parameters:

A) $\alpha_i \neq 0$, (there are year effects on survival),
B) $\alpha_i \equiv 0$, (there are no year effects on survival).

Table 2

Deviance information criterion and index of model complexity (p_D) for 16 models described in the text. Symbols "+" and "−" indicate presence or absence of effect in the model.

Model	p_D	DIC	Recruitment		Annual variation		Age effects on survival		
			Trend	Egg coll	Recruit	Survive	β_1	$\beta_2, \beta_3, \beta_4, \beta_5$	β_6
CAAE	68.3	1732.7	+	−	+	+	−	−	−
CAAC	71.6	1739.0	+	−	+	+	+	−	−
CAAD	72.5	1755.6	+	−	+	+	−	−	+
CAAB	75.9	1775.4	+	−	+	+	+	−	+
CAAA	95.9	1817.4	+	−	+	+	+	+	+
DAAA	96.8	1817.8	+	+	+	+	+	+	+
AAAA	101.7	1823.7	−	+	+	+	+	+	+
BAAA	102.2	1827.0	−	−	+	+	+	+	+
CABA	56.9	1873.8	+	−	+	−	+	+	+
AABA	62.9	1881.2	−	+	+	−	+	+	+
BABA	63.3	1884.9	−	−	+	−	+	+	+
BBAA	62.1	1915.5	−	−	−	+	+	+	+
ABAA	62.7	1930.3	−	+	−	+	+	+	+
CBAA	48.7	1949.5	+	−	−	+	+	+	+
ABBA	24.0	1970.9	−	+	−	−	+	+	+
BBBA	23.2	1983.6	−	−	−	−	+	+	+

The fourth letter describes restrictions on the age effects on survival:

A) no restrictions,
B) $\beta_2 = \beta_3 = \beta_4 = \beta_5$,
C) $\beta_2 = \cdots = \beta_6$,
D) $\beta_1 = \cdots = \beta_5$,
E) $\beta_1 = \cdots = \beta_6$.

We used the deviance information criterion (DIC) (Spiegelhalter et al., 2002) as a guide for comparing models. DIC consists of a measure of fit, the posterior mean of the deviance

$$D(\text{Parameters}) = -2\ \text{loglikelihood}(\text{Parameters}; \text{Data})$$

plus a measure of model complexity, p_D, described by Spiegelhalter et al. (2002) as the "effective number of parameters." This latter quantity is calculated as the posterior mean of $D(\cdot)$ minus the value of D calculated at the posterior mean value of the parameters. The log likelihood used in these calculations was based on the marginal distribution $[\boldsymbol{B}, \boldsymbol{W} \mid \boldsymbol{\theta}]$. Models with small values of DIC are favored on the grounds of parsimony. Values are tabulated in Table 2.

Table 3

Posterior means and standard deviations for age-specific survival rates

<table>
<tr><th>Model</th><th>$\varphi_{\cdot 1}$</th><th>$\varphi_{\cdot 2}$</th><th>$\varphi_{\cdot 3}$</th><th>$\varphi_{\cdot 4}$</th><th>$\varphi_{\cdot 5}$</th><th>$\varphi_{\cdot 6}$</th></tr>
<tr><td>CAAA</td><td>0.894
(0.023)</td><td>0.908
(0.023)</td><td>0.922
(0.024)</td><td>0.936
(0.023)</td><td>0.944
(0.023)</td><td>0.890
(0.014)</td></tr>
<tr><td>CAAB</td><td>0.895
(0.023)</td><td colspan="4">0.931
(0.012)</td><td>0.892
(0.014)</td></tr>
<tr><td>CAAC</td><td>0.900
(0.021)</td><td colspan="5">0.910
(0.010)</td></tr>
<tr><td>CAAD</td><td colspan="5">0.922
(0.011)</td><td>0.892
(0.014)</td></tr>
<tr><td>CAAE</td><td colspan="6">0.910
(0.010)</td></tr>
</table>

7. Results and Discussion

For each model fitted, we generated 4 Markov chains of length 60000, discarding the first 10,000 values as a burn-in, and approximating features of the posterior distributions using the remaining 4 sets of 50,000 values. The Markov chains exhibited good mixing, and only moderate autocorrelation. Features of the posterior distributions are summarized in Table 3; we denote the inverse of the logit transformation by $\text{expit}(x) = \exp(x)/(1 + \exp(x))$.

We began by fitting models *AAAA* and *BAAA*, looking to see whether there is any evidence on recruitment of an effect due to egg collection. There having been no formal experiment conducted, the "treatment" of egg collection not having been applied to a random set of years, and the types and intensity of manipulation having varied through time, there can be no unequivocal answer to the question of egg collection's effects on the population. The posterior probability that $a_1 < a_0$ under model *AAAA* was 0.966, indicating that recruitment was lower in egg-collection years, as has been suggested. However, a plot of the posterior means of λ_i against time strongly suggests a declining trend in recruitment (Figure 2), which could reasonably be explained as a density-dependent effect related to the increasing population size. The apparent difference in parameters a_0 and a_1 could be an artifact of this trend. We thus fit models *CAAA* and *DAAA*, allowing trend in recruitment. Measured by DIC, both of these models fit better and were less complex than either *AAAA* or *BAAA*. The effect of egg collection under model *DAAA* was negligible (difference of intercepts estimated as 0.033, with posterior standard deviation 0.160). Thus, we favor models with trend in recruitment but no effects due to egg collection.

The additional model complexity due to incorporating yearly stochastic variation in recruitment rates was more

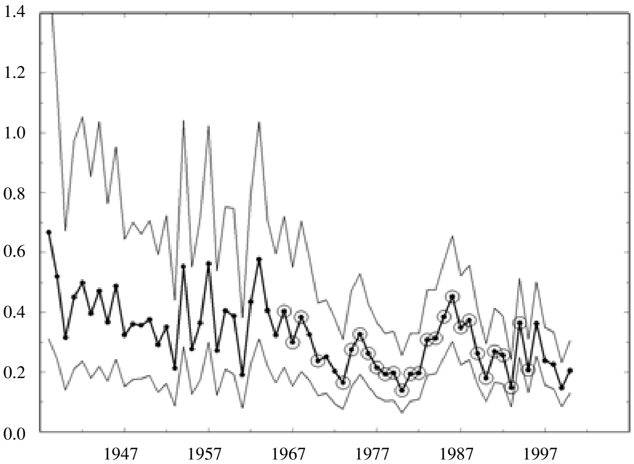

Figure 2. Posterior means and 95% credible intervals for per-breeder recruitment rates λ_i, plotted against year, with egg-collection years in bold. Results are for model *AAAA*.

than offset by gains in fit; DIC values for *AAAA*, *BAAA*, and *CAAA* were consistently smaller than those for *ABAA*, *BBAA*, and *CBAA*. Similarly, we conclude that a better fit is provided by including year effects on survival; DIC values for *AAAA*, *BAAA*, and *CAAA* were consistently smaller than those for *AABA*, *BABA*, and *CABA*. Figure 3 suggests that there may be some pattern of increasing survival rates through time.

Estimates of age-specific survival rates under models *CAAA*, *CAAB*, *CAAC*, *CAAD*, and *CAAE* are given in Table 3; the value $\varphi_{\cdot j}$ is the average value of $\text{expit}(\alpha + \beta_j)$ over realizations of year effects α, sampled from a mean-zero normal distribution with precision τ_α. The best fitting

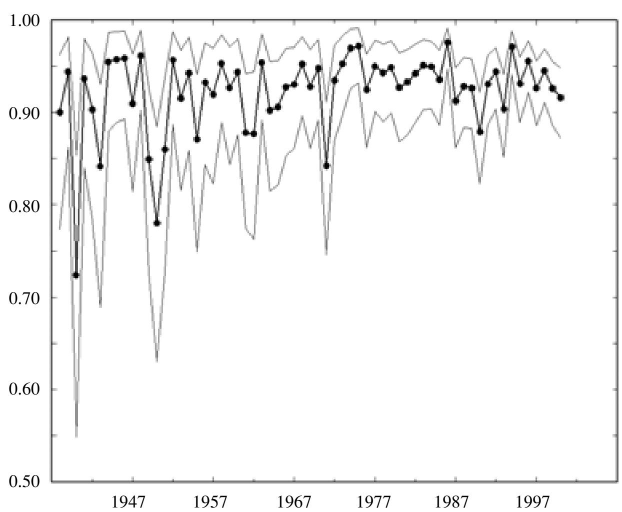

Figure 3. Posterior means and 95% credible intervals for average survival rates $\varphi_{i\cdot}$, plotted against years. Results are for model *CAAA*, with $\varphi_{i\cdot} = \text{expit}(\alpha_i + \beta_\cdot)$, with $\beta_\cdot = \frac{1}{6}\sum_{j=1}^{6} \beta_j$.

Table 4

Estimates of parameters, other than age effects β_j, under models CAAA and CAAE (posterior means and 95% credible intervals).

	CAAA		*CAAE*	
	Mean	95% CI	Mean	95% CI
a	−1.108	(−1.263, −0.961)	−1.116	(−1.266, −0.971)
b	−0.018	(−0.026, −0.010)	−0.018	(−0.026, −0.010)
$\tau_\lambda^{-1/2}$	0.366	(0.230, 0.524)	0.366	(0.231, 0.522)
$\tau_\alpha^{-1/2}$	0.680	(0.481, 0.916)	0.661	(0.462, 0.897)

Parameters a and b are intercept and slope in regression of log(recruitment rate) on time (equation [5]); $\tau_\lambda^{-1/2}$ and $\tau_\alpha^{-1/2}$ are standard deviations for year effects related to recruitment and survival.

model, based on DIC, is *CAAE* (Table 2), which assumes that there is no age-specific variation in survival. The existence of age-specific variation in survival seems likely on biological grounds, and the pattern indicated by estimates under model *CAAA* seems reasonable. We note that the credible intervals for the age effects overlap, and suggest that the selection of *CAAE* by *DIC* is thus an artifact of model selection on the basis of parsimony and the limited nature of the data analyzed. We thus regard model *CAAA* as the most appropriate for presentation. We note that posterior means and 95% credible intervals for parameters other than β_j's are nearly identical under models *CAAA* and *CAAE* (Table 4).

While the survival and recruitment rates are of primary interest in our analysis, it is worth noting that inference can be made about the age distribution in any given year. Thus, for instance, under model *CAAA* we may infer that, of the 161 white birds observed in the 2001 census, roughly 91 were in age class 7. A summary of the posterior distributions for the year 2001 age distribution is given in Table 5. The shortness of the credible intervals for the numbers of individuals in age classes (Y_{ij}) is a reflection, not only of the precision with which the parametric model has been estimated, but also of the substantial information provided by the age-structured transition model.

To describe the survival function for individual birds, we predicted lifetimes using the posterior distribution calculated under model *CAAA*. Each lifetime is described by a sequence

Table 5

Posterior summaries for year 2001 *age distribution: posterior mode, credible interval (shortest interval containing at least* 95% *mass), and posterior probability of CI*

	Numbers of individuals in age class		
Age class	Mode	CI	Probability
1	15	[15, 15]	1
2	8	[7, 9]	0.991
3	14	[12, 16]	0.975
4	14	[12, 17]	0.974
5	21	[18, 24]	0.959
6	12	[9, 14]	0.966
7	91	[87, 97]	0.964

of independent Bernoulli trials S_j, with parameters φ_j^*. These are calculated as

$$\varphi_j^* = \mathrm{expit}\big(\alpha_j^* + \beta_j\big), \quad \text{for } j = 1, 2, \ldots, 6, \text{ and}$$
$$\varphi_j^* = \mathrm{expit}\big(\alpha_j^* + \beta_6\big), \quad \text{for } j = 7, 8, \ldots,$$

where α_j^* is sampled from a mean-zero normal distribution with precision τ_α; the values β_j and τ_α are sampled from their joint posterior distribution. The lifetime X is the minimum index j for which $S_j = 0$; since our analysis was conditional on birds having reached age-class 1 (i.e., having successfully fledged and survived to the first winter), the inferences we present are conditional on $X \geq 1$. We reach the following conclusions about the life distribution of individual birds, conditional on their having been counted as brown juveniles: 43.7% die before reaching age-class 7, and 50.2% die before reaching age 8; the 99th percentile is age 38.

We calculated a predictive distribution for the population in year 2002 (i.e., the posterior distribution of Y_{65}). Using the posterior modes and 90% credible intervals, we predicted a population size of 179 (158, 193) including 17 (9, 30) new recruits.[1]

Our choice of a mean-zero normal distribution, with $\tau_\beta = 0.40$, for age-effects β_j was motivated by three considerations. First, the distribution of expit(β_j) thus induced is nearly uniform (quantiles 0.50, 0.60, 0.70, 0.80, 0.90, and 0.95 are 0.500, 0.599, 0.696, 0.791, 0.884, and 0.931, respectively). Second, we found that our implementation of MCMC using the informative prior produced Markov chains of superior stability to those produced with $\tau_\beta = 0$. Finally, we note that the posterior distributions of β_j's were largely unaffected by the choice of prior. Under model *CAAE,* with $\tau_\beta = 0.40$, the posterior mean and standard deviation of β were 0.916 and 0.011, and the 95% credible interval was (0.899. 0.932). With $\tau_\beta = 0$, the posterior mean and standard deviation of β were 0.917 and 0.011, and the 95% credible interval was (0.900, 0.933).

Our analysis can be summarized as follows: first, we described the set of age distributions Y_i, $i = 1, 2, 3, \ldots, n$, as a multivariate time series, conditioning on the counts of white and brown birds in year 1, W_1 and B_1, and conditioning on the demographic parameters of interest. Specification of prior distributions for the demographic parameters leads to a Gibbs sampling scheme for the joint posterior distribution of the demographic parameters and the unobserved age distributions Y_i, given the annual counts of brown and white birds. The precision with which we were able to estimate population parameters is due, in part, to the fact that we were working with complete counts of the population. We envision the extension of the techniques described here to incomplete counts, especially when auxiliary data are available for the estimation of detection rates.

Acknowledgements

We thank the associate editor and two anonymous referees for extraordinarily helpful comments and careful reviews.

[1] The population size in 2002 turned out to be 184, including is new recruits (Tom Stehn, personal communication).

Résumé

L'analyse démographique des populations structurées en âge repose soit sur l'analyse d'histoires individuelles, soit lorsque les animaux ne sont pas identifiés individuellement, sur une information sur les nombres d'individus passant d'une classe d'âge à une autre au cours du temps. S'il est la plupart du temps difficile de déterminer l'âge exact d'un individu pris au hasard, il est en revanche souvent possible d'assigner un individu à une classe d'âges. Par exemple, il est souvent possible de distinguer les oiseaux âgés d'un an des plus vieux. Dans ces cas, la structure en âges de la population peut être considérée comme une variable latente gouvernée par un processus a priori, et les données sont alors un résumé de cette structure latente. Nous étudions ici le problème de la reconstitution de la structure latente et de l'estimation des paramètres du processus à partir de résumés d'information sur les classes d'âges. Nous présentons une analyse démographique de la population migrante de la grue américaine (*Grus americana*), actuellement en voie d'extinction, basée uniquement sur des comptages des oiseaux d'un an et des oiseaux plus âgés. Nous estimons des taux de survie en fonction de l'âge et de l'année. Nous apportons des éléments à la controverse sur l'impact de la gestion des terrains de reproduction sur le taux de recrutement, en reliant le taux de recrutement au nombre d'oiseaux de sept ans et plus, et en analysant les variations au cours du temps de ce taux.

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Received July 2002. *Revised June* 2003.
Accepted June 2003.

Appendix

Gibbs Sampling of the Population History

The process we used for sampling the population history is best illustrated by example. From Table 1, we see that there were 10 brown and 62 white birds in 1977, 7 brown and 68 white birds in 1978, and 6 brown and 70 white birds in 1979. Since there were 72 birds alive in 1977, all of which would have been white in 1978, had they survived, we can deduce that there were 4 deaths. Generation of a candidate value for Y_i consists of randomly assigning those deaths to age classes; we do so, subject to the constraint of consistency with the current values of Y_{i-1} and Y_{i+1}. Suppose that the current values of Y_{i-1} and Y_{i+1} are as given in Table A.1. Between 1977 and 1978, there could have been 0, 1, or 2 deaths among the 10 age class 1 birds, but no more, since the number of age class 2 birds in 1978 must be at least 8 for consistency with age class 3 in 1979. Similarly, we obtain upper bounds on the numbers of 1977–1978 deaths in age classes 2, 3, and 4; these are 1, 0, and 0, respectively. The 43 birds in age classes 5, 6, and 7 in 1977 would all be in age class 7 in 1979, if they survived twice; hence we obtain an upper bound of $43 - 37 = 6$ for the 1977–1978 deaths in these 3 age classes. We note also that, since the sum of the upper bounds for deaths in age classes 1 to 4 is only 3, and there were four total deaths, there must have been at least 1 death in age classes 5 to 7.

Table A.1
A set of age distributions consistent with the data for 1977–1979*. Bold values for* 1978 *are candidate value generated consistently with values for* 1977 *and* 1979*, as described in the Appendix*

	Age class						
Year	1	2	3	4	5	6	7
1977	10	12	5	2	2	3	38
1978	7	**9**	**12**	**5**	**2**	**1**	**39**
1979	6	7	8	11	5	2	37

The upper bounds on numbers of deaths for age classes 1, 2, 3, 4, and 5 through 7 are 2, 1, 0, 0, and 6 respectively. We thus place two balls labeled "age class 1," one labeled "age class 2," and six labeled "age classes 5 through 7" in an urn, and draw 4 (the total number of deaths) at random without replacement. Suppose that our draw yields one labeled "age class 1" and three labeled "age classes 5 through 7." The three must be allocated to age classes 5 through 7, consistent with the numbers for 1977. We thus place 2,3, and 38 balls labeled "age class 5," "age class 6," and "age class 7" in a second urn, and draw 3 at random without replacement. Suppose that this second draw yields one ball labeled "age class 5" and two labeled "age class 7"; we conclude that the numbers of 1977–1978 deaths in the 7 age classes were 1,0,0,0,1,0, and 2. The candidate value for Y_i is obtained by subtraction of these deaths from the corresponding cells of Y_{i-1}, it is highlighted in Table 6.

The candidate-generating procedure is modified slightly for several special cases. For $i = n$, the upper bounds on year $n-1$ deaths for the various age classes are simply the numbers of individuals in the various age classes. For $i = 1$, given the current value of Y_2, we may determine how many of the 3 year-1 deaths were in age class 1, and randomly assign the other deaths to the remaining age classes.

Finally, we note that, in certain years or blocks of years, there were no deaths (1944–1946, 1948, 1952, 1974–1975); for these years $D_i = (W_i + B_i) - W_{i+1} = 0$ (see Table 1). If there were no deaths in year i, Y_{i+1} is completely determined by B_{i+1} and Y_i. The algorithm we have described for producing candidate values Y_i requires consistency with current values of Y_{i-1} and Y_{i+1}, hence it cannot produce a candidate value different from the current value when $D_i = 0$. The solution to this difficulty is to generate candidate values for groups of years in a manner similar to that previously described for individual years. Thus, for instance, a candidate value for 1974 was generated consistent with the constraints imposed by current values for 1973 and 1977, and used to determine the corresponding candidate values for 1975 and 1976.

The procedure we have described generates candidate values consistent with the range constraints imposed by the model. The candidate value is then accepted or rejected with probability given by equation (9).